

## ***Speyeria atlantis* Phenotypes in the Southern Rocky Mountains (Lepidoptera: Nymphalidae: Argynninae)<sup>1</sup>**

Clifford D. Ferris<sup>2</sup>

Bioengineering Program, University of Wyoming, Laramie, Wyoming 82071

**Abstract.** Phenotypes of *Speyeria atlantis* found along the Front Range of the Rocky Mountains from southeastern Wyoming to north-central New Mexico are described and discussed.

### **Introduction**

The first publication to detail the distribution of *Speyeria atlantis* (W. H. Edwards) along the Colorado Front Range was by Brown, Eff & Rotger (1955, 1957). Subsequently, A. H. Moeck (1957, 1975) published a monograph on the geographic variability of *Speyeria* in North America. He included a general discussion of *S. atlantis* in the Rocky Mountain region. Since Moeck's monograph appeared, extensive collecting in Wyoming, Colorado and New Mexico by numerous individuals has greatly extended our knowledge of the distribution of this insect. A brief treatment covering Wyoming was published by Ferris (1971), and a summary of contemporary information can be found in Ferris & Brown (1981). A very much expanded discussion from this latter work is now presented.

### **Taxonomic Background**

In the region encompassed by this paper, *Speyeria atlantis* occurs in appropriate habitats from 5900' (1800 m) to timberline at roughly 12,000' (3660 m) in southern Colorado. In southern Wyoming, timberline begins at about 10,800' (3295 m). *Viola* species serve as the larval hosts, and *atlantis* may be found in riparian canyons, mountain meadows, and wooded areas in association with these plants. Adults are particularly attracted to nectar sources belonging to the mint family, especially wild bergamont (*Monarda* sp.). These butterflies behave rather differently in different geographic localities, apparently indicative of adaptation to local ecological conditions involving their larval hosts.

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<sup>2</sup>Research Associate: Allyn Museum of Entomology/Florida State Museum, Sarasota, Florida; Florida State Collection of Arthropods, Division of Plant Industry, Florida Dept. of Agriculture and Consumer Services, Gainesville, Florida. Research Associate in Entomology: Los Angeles County Museum of Natural History, Los Angeles, California.

Four distinct forms of *S. atlantis* occur along the Front Range; three of which have been given subspecific recognition. In addition, various clines or intergrades can be identified.

The first subspecies to be named was *hesperis* (W. H. Edwards), 1864. This was followed by *electa* (W. H. Edwards), 1878, and finally *nikias* (Ehrmann), 1917. In 1892, W. H. Edwards also named *cornelia*, now considered by most specialists to be a synonym of *electa*. As is the case with many butterflies named during the 1800s, the type localities of these *atlantis* subspecies were somewhat vague.

In 1947, dos Passos & Grey published a paper in which they attempted to fix the type localities of all of the North American *Speyeria*, and to identify holotypes, or designate lectotypes or neotypes as the case required. In 1965 as part of his continuing series of monographs on the W. H. Edwards butterfly names, Brown re-examined and revised some of the conclusions reached by dos Passos & Grey. The current designation of type localities as it appears in Miller & Brown (1981) is as follows: *hesperis*, Turkey Creek Junction, Jefferson Co., Colorado (fixed by dos Passos & Grey, confirmed by Brown); *electa*, Turkey Creek Junction, Jefferson Co., Colorado (fixed by dos Passos & Grey as Rocky Mountain National Park, Colorado, and revised by Brown); *nikias*, Jemez Springs, Sandoval Co., New Mexico; *cornelia*, Ouray, Ouray Co., Colorado (fixed by dos Passos & Grey, confirmed by Brown).

The basis upon which Brown changed the type locality for *electa* rests upon the fact that T. L. Mead, who collected the type specimen in 1871, did not collect in the region now occupied by Rocky Mountain National Park. This insect, however, does occur in the Park.

From my field experience, I doubt that the type of *nikias* came from Jemez Springs, *per se*. More likely, it was taken at higher elevation a few miles to the north in the Jemez Mts., where these butterflies abound at the edges of forest clearings.

The fixation of type localities by Brown has generated a problem in that two subspecies now have the same type locality. This raises the following question: If *atlantis*, in fact, is a valid biological species, then how can two distinct subspecies occur at the same locality? Given our present knowledge several answers may apply. An obvious one is simply that one of the type localities is incorrect. Both *hesperis* and *electa* phenotypes, however, do occur sympatrically and synchronously in many areas. Thus the types that represent both taxa may indeed have been collected in the same locality. Another answer is that *hesperis* and *electa* are sibling species in the "*atlantis* complex". Rearing studies, which have yet to be carried out (see below), should prove or disprove this theory. A third answer is that *atlantis* along the Front Range is polymorphic. My own field studies indicate that this is an attractive possibility substantiated in part by data subsequently presented.

The obvious solution to the questions and answers posed above would be provided by controlled rearing studies in the laboratory. This solution is not so simple as it appears. Techniques for rearing *Speyeria* have been published (Mattoon, et al., 1971), but persons attempting to rear *S. atlantis* have experienced various difficulties. G. D. Willis (pers. comm.) has experienced little difficulty in rearing the larvae to adults once ova were obtained. He has found *atlantis* females from eastern North America to be very reluctant to oviposit in captivity. Gravid females that I sent to him of the Wyoming *hesperis* and *electa* phenotypes refused to oviposit.

Sterling O. Mattoon (*in litt.*) has reared Rocky Mountain *atlantis*, but ova and larvae were not segregated as to female parent. Thus clear data are not available. It is his impression from controlled rearing of ova from other populations that adult series are polymorphic to some degree. He cites as the probable cause the differences between environmental conditions in the laboratory and in nature, and multiple matings of the females with different males.

On the other hand, L. P. Grey (*in litt.*) has stated that the reared series of *Speyeria* that he has examined tend to follow the phenotype of the female parent. Thus we have equivocal results from the rearing attempts that have been conducted to date.

What is needed is a series of laboratory experiments in which virgin females are hand-paired with males, so that the phenotypes of both parents are clearly known. Wild-caught pairs *in copulo* will not suffice, since the number of matings that the females have experienced cannot be determined, except by dissection, and this procedure would not identify male phenotype. In some nymphalids, the ova are fertilized only by the last mating and wild-caught pairs would suffice; however it is not known if this is the case with *Speyeria*. Mattoon stated that he has had no success in attempts to hand-pair *Speyeria*. Thus for the present, we must rely upon field data.

### Discussion of Principal Phenotypes

The main character by which the *atlantis* phenotypes in the Front Range are separated lies in the discal area of the ventral hind wings. Both discal color and the nature of the pale spots are used. In *hesperis*, the disc is medium brown, and the spots are cream-colored and opaque. The disc in *electa* is dark brown (almost purplish-brown in some fresh specimens) beset with bright silver spots. The disc in *nikias* is red-brown or brick-red, and the spots are silvered. Of the Front Range phenotypes, *electa* is the closest to the "parent" or Appalachian population. Nominate *atlantis* occurs in the northeastern United States and in southeastern Canada in Canadian zone or boreal environments. A relict population exists in the Black Hills refugium in western South Dakota and northeastern Wyoming. A fourth phenotype, to be discussed subsequently, occurs in Las Animas



Co., Colorado and adjacent Colfax Co., New Mexico.

In most cases, *hesperis* is a low-elevation insect associated with riparian canyons, although it may be taken throughout the Transition zone and into the lower Canadian zone. It is often out in the open nectaring at thistles in meadows, and at various members of the mint family along streams. I have taken specimens at 9500' (2900 m) in the Snowy Range, Albany Co., Wyoming, but *hesperis* is usually encountered at elevations from 5900-8500' (1800-2600 m). Figures 1-2 illustrate *hesperis*.

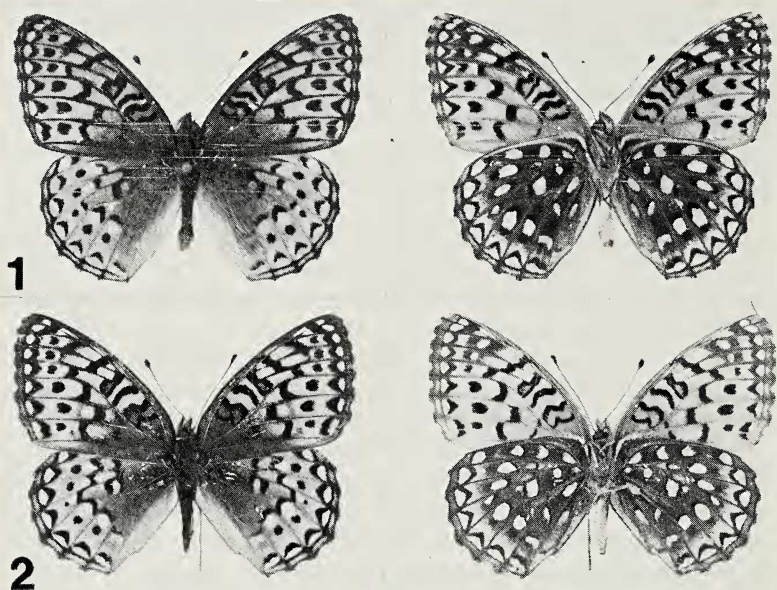


Fig. 1. *S. atlantis hesperis* male, D (left), V (right). Boulder Can., Boulder Co., CO, 21 vii 65.

Fig. 2. *S. atlantis hesperis* female, D (left), V (right). Flagstaff Mt., Boulder Co., CO, 7 viii 68.

Inormally ssociate the *electa* phenotypes with forest roads and the edges of forest clearings at elevations above 8000' (2440 m). In southern Wyoming, it occurs sympatrically and synchronously with *hesperis* at approximately 8200' (2500 m) in the Sherman Range of the Laramie Mts., the Snowy Range, and the east slope of the Sierra Madre Mts. The vegetative association is aspen-conifer. Figures 3-4 illustrate *electa*.

The *nikias* phenotype is generally distributed along the Western Slope in Colorado, rather than in the Front Range. On the west slope of the Sierra Madre Mts., Carbon Co., Wyoming, specimens referable to *nikias* can be taken along with *hesperis* and *electa* forms. The vegetative association is oak-aspen-conifer. South of this region on a line through Rabbit Ears Pass,



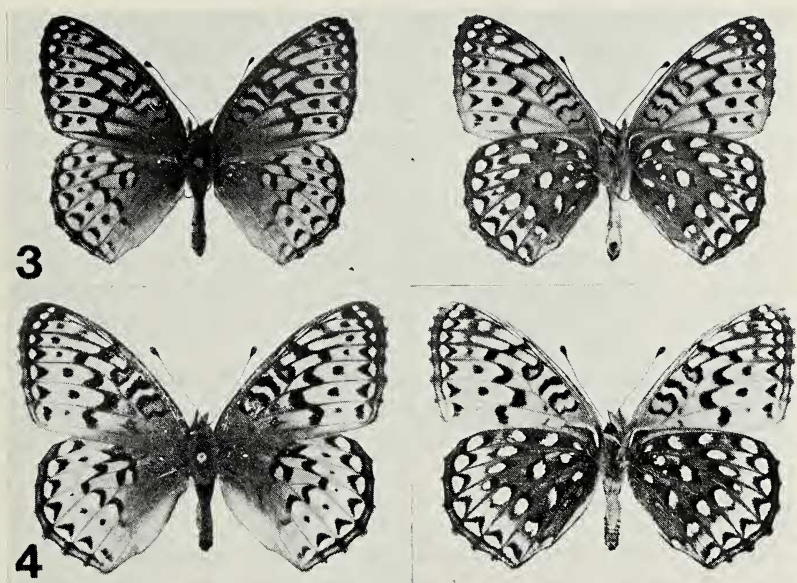


Fig. 3. *S. atlantis electa* male, D (left), V (right). Pole Mt., Medicine Bow Nat. For., Albany Co., WY, 18 vii 71.

Fig. 4. *S. atlantis electa* female, D (left), V (right). Foxpark, Albany Co., WY, 1 viii 69.

Routt Co., Colorado and along the Western Slope, *nikias* is the predominant form, although the *electa* phenotype is frequently encountered. The *nikias* phenotype usually flies in aspen-conifer regions, and I have seen it at timberline at the base of Mt. Uncompahgre in Hinsdale Co., Colorado. This butterfly occurs at the edges of forest clearings in aspen-conifer habitat in Rio Arriba, Santa Fe and northern Sandoval Cos., New Mexico. The typical altitude range in New Mexico is 7900-8500' (2400-2600 m). Figures 5-6 illustrate *nikias* from the Jemez Mts.

The most distinctive of the four phenotypes occurs in the high mesa regions to the northeast of Raton, New Mexico. The vegetative association where I have taken this butterfly is oak-conifer. The adults normally remain well inside the forested areas, rather than out in the open meadows, and fly in the sunshine and shadow of the forest glades. Both *Rudbekia* sp. and thistles are favored nectar sources.

This phenotype is the palest colored *atlantis* that I have encountered. In facies, flight pattern, and general habits, it is very similar to the subspecies *greyi* Moeck from Elko Co., Nevada, although somewhat larger and paler yet than *greyi*. Adults of both sexes tend to flutter close to the ground through the vegetation, and frequently perch on the ground, a characteristic also of *greyi*. When startled, however, they are determined fliers as in

other subspecies of *atlantis*. Figures 7-8 depict this phenotype.

Ferris (in Ferris & Brown, 1981, p. 311) stated regarding this pale phenotype: "The variation within a given colony is too great to consider assigning subspecific status to this entity". Until the problems of speciation and polymorphism in *atlantis* are resolved, it seems unwise to erect additional subspecific taxa in this complex. While this paper was undergoing initial review, however, Scott (1981) proposed the name *ratonensis* for the pale phenotype. It is not clear that this publication meets all of the requirements of the Code of the I.C.Z.N. The designated holotype from Raton Mesa, Colfax Co., New Mexico is apparently deposited in the collection of the Los Angeles County Museum of Natural History, Los Angeles, California.

Various intergrade or clinal forms among the four principal phenotypes are regularly encountered. These will be discussed in the next section which treats the distribution of the *atlantis* complex in the central Rocky Mountain region.

### Distribution of Phenotypes

Figure 9 shows the distribution of *S. atlantis* phenotypes in the geographic region of interest. Two other subspecies occur in New Mexico:

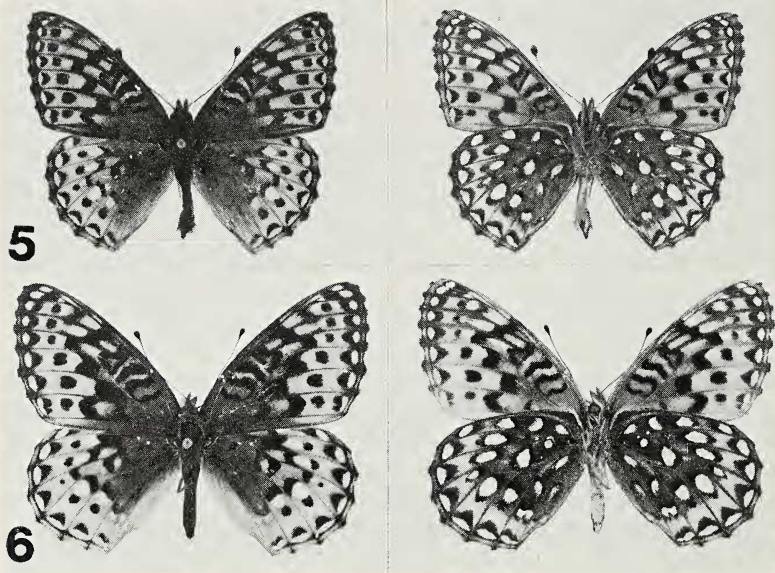


Fig. 5. *S. atlantis nikias* male, D (left), V (right). Clear Creek C. G., Santa Fe Nat. For., Rio Arriba Co., NM, 10 vii 79.

Fig. 6. *S. atlantis nikias* female, D (left), V (right). Clear Creek C. G., Santa Fe Nat. For., Rio Arriba Co., NM, 10 vii 79.

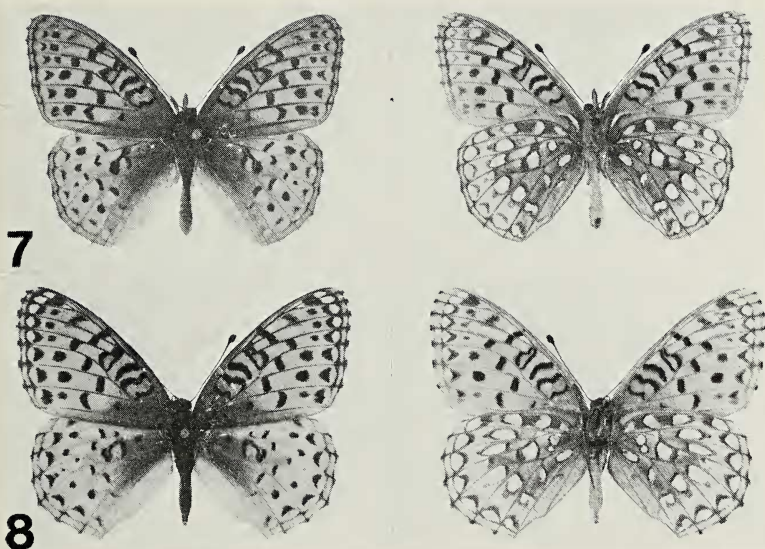


Fig. 7. *S. atlantis* pale phenotype male, D (left), V (right). Upper Sugarite Canyon, Las Animas Co., CO, 4-5 viii 81.

Fig. 8. *S. atlantis* pale phenotype female, D (left), V (right). Upper Sugarite Canyon, Las Animas Co., CO, 4-5 viii 81.

*dorothea* Moeck, just to the south of where the map ends, and *nausicaa* (W. H. Edwards) in the southwestern part of the state. These subspecies do not interact to any extent with the butterflies under discussion, and will not be further mentioned. Other non-interacting subspecies occur to the north and west of the region illustrated.

From the map, it is clear that *hesperis* generally occupies the Colorado Front Range, and *nikias* the Western Slope. Above 8000' (2440 m), *electa* may be found on either side of the Continental Divide in both Colorado and Wyoming. In New Mexico, west of the southern extension of the Sangre de Cristo Mts., and into the Jemez Mts. in Rio Arriba, Santa Fe and northern Sandoval Cos., we find *nikias*. The pale phenotype *ratonensis* occurs in basically undiluted form in extreme northeastern Colfax Co., New Mexico and into the contiguous portion of southern Las Animas Co., Colorado.

Over most of Taos Co. and extreme western Colfax Co., New Mexico, the predominant form is an intermediate between *nikias* and *electa*. The spots on the disc are silvered, and the ground color is generally dark, occasionally with some basal olivaceous scaling (Cabresto Canyon, Taos Co.). On an individual basis, many specimens are referable to *nikias*, but when taken in series intermediate forms are apparent.



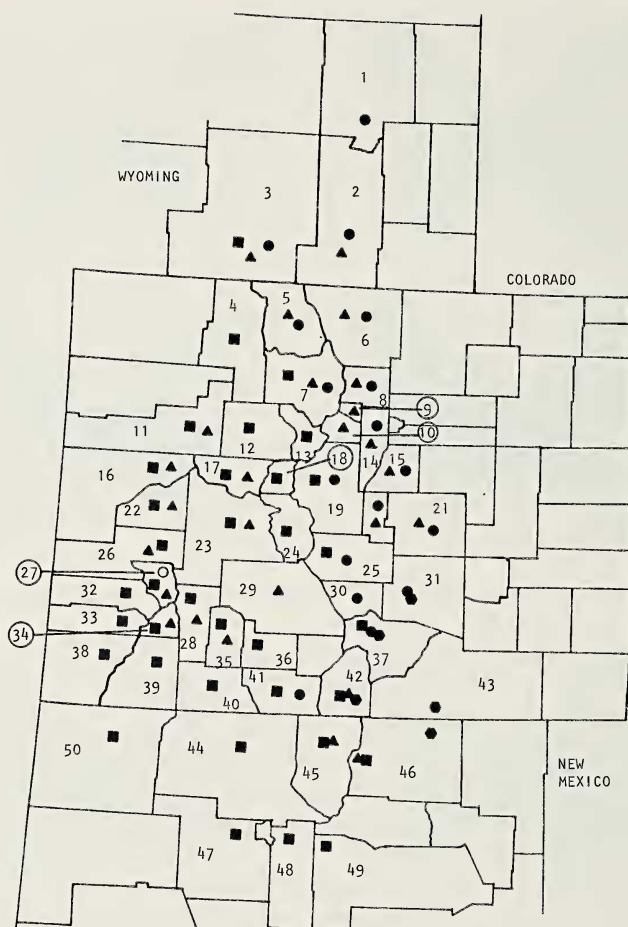
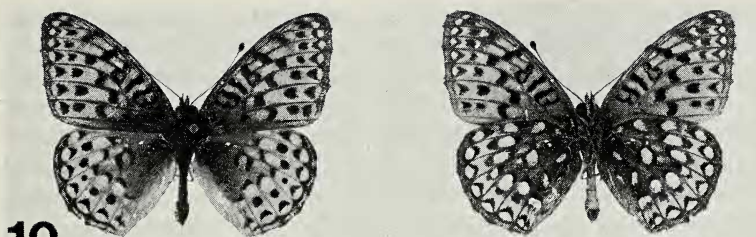
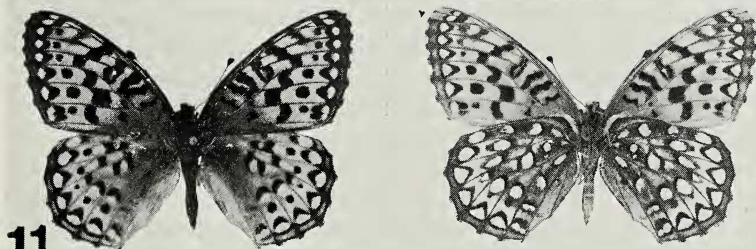


Fig. 9. Distribution of *S. atlantis* in southern Wyoming, Colorado and northern New Mexico. Solid dots = *hesperis*; triangles = *electa*; squares = *nikias*; hexagons = pale phenotype. Conjoined symbols emphasize clines. County names corresponding to map numbers: 1. Converse, 2. Albany, 3. Carbon, 4. Routt, 5. Jackson, 6. Larimer, 7. Grand, 8. Boulder, 9. Gilpin, 10. Clear Creek, 11. Garfield, 12. Eagle, 13. Summit, 14. Jefferson, 15. Douglas, 16. Mesa, 17. Pitkin, 18. Lake, 19. Park, 20. Teller, 21. El Paso, 22. Delta, 23. Gunnison, 24. Chaffe, 25. Fremont, 26. Montrose, 27. Ouray, 28. Hinsdale, 29. Saguache, 30. Custer, 31. Pueblo, 32. San Miguel, 33. Dolores, 34. San Juan, 35. Mineral, 36. Rio Grande, 37. Huerfano, 38. Montezuma, 39. La Plata, 40. Archuleta, 41. Conejos, 42. Costilla, 43. Las Animas, 44. Rio Arriba, 45. Taos, 46. Colfax, 47. Sandoval, 48. Santa Fe, 49. San Miguel, 50. San Juan. Open symbol = dubious record.



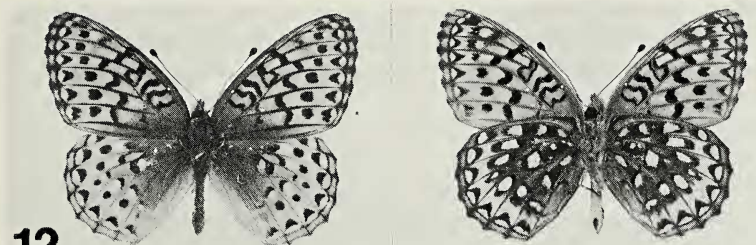
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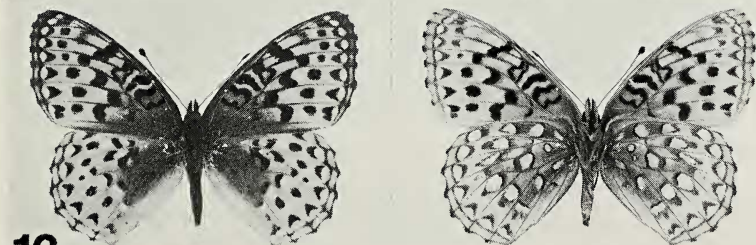
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Fig. 10. *S. atlantis* male, D (left), V (right). La Veta Pass, Huerfano/Costilla Co., CO, 3 viii 81.

Fig. 11. *S. atlantis* female, D (left), V (right). La Veta Pass, Huerfano/Costilla Co., CO, 3 viii 81.



**12**



**13**

Fig. 12. *S. atlantis* intermediate disc male, D (left), V (right). Cuchara Canyon, Huerfano Co., CO, 3-4 viii 81.

Fig. 13. *S. atlantis* pale disc female, D (left), V (right). Cuchara Canyon, Huerfano Co., CO, 3-4 viii 81.

In some respects, *nikias* is an unfortunate taxon. Material from the Jemez Springs region exhibits considerable variability, and not the stability of phenotype normally associated with a subspecific entity. Thus we must apply the name *nikias* in a broad sense and not in a strict sense.

Moving northward into Costilla Co., Colorado, both *nikias* and *electa* phenotypes have been recorded. In the vicinity of La Veta Pass in northeastern Costilla Co. and roughly central Huerfano Co., a cline exists, examples of which are shown in Figures 10-11. These butterflies generally have silver spots, but some individuals, females especially, may have partially silvered or opaque spots. Discal color is generally medium brown as in *hesperis*, darkening in some specimens to that of *electa*. An occasional pale specimen may be taken. In this region, the butterflies appear to prefer heavily wooded areas, but they may occasionally be taken in the open along streams and at the edges of clearings.

A curious blending of phenotypes occurs in southwestern Huerfano Co. from Cuchara Canyon (9100', 2775 m) eastward to Cordova Pass (formerly called Apishapa Pass, 11,000', 3350 m). Both silvered and unsilvered forms occur, and the discal color ranges from as pale as *ratonensis* to as dark as typical *nikias*. Typical specimens are illustrated in Figures 12-13. In this region, the butterflies are sometimes taken in open meadows near streams, but they seem to prefer heavily wooded areas. Thistles are a favored nectar source. Figure 14 shows a dark-disc specimen from Cuchara Canyon.

Dark-disc specimens are very rare in the *ratonensis* population. Based upon my field work, they represent about two percent of the total. In these cases, the discal color approximates that of a pale *hesperis*. Figure 15 shows a dark-disc specimen from Sugarite Canyon near Raton, New Mexico.

In the Rockies, occasionally unsilvered specimens are recorded from normally silver-spotted populations of *atlantis*. This perhaps accounts for records of *hesperis* from the Western Slope in Ouray Co., Colorado. along the Front Range, specimens with partially silvered spots occur frequently, especially in the females. Material from extreme western Colorado occasionally exhibits some influence from the red-disc paler forms found in southern Utah and northern Arizona.

## Conclusions

Field data at hand produce a mixed picture of the *Speyeria atlantis* complex in the geographic region under discussion. Results from rearing attempts to date are inconclusive. In the northern portion of the region (Sierra Madre Mts., Carbon Co., Wyoming), field-collected specimens are indicative of a cline that runs from *hesperis* through *electa* to *nikias*. Two apparent parallel clines exist in the southern portion of the region. In Taos Co., New Mexico, the *nikias* and *electa* phenotypes form the two ends of a



cline. In southeastern Colorado, the cline runs from the pale *ratonensis* phenotype through *hesperis* and *electa* into *nikias*.

Preliminary enzyme electrophoresis studies were conducted by Angela F. Tebaldi, a graduate student at the University of Wyoming (1982). The enzymes extracted from ground preparations of adult *Speyeria atlantis* specimens and subjected to electrophoresis separation were: malic dehydrogenase, malic enzyme, glutamate dehydrogenase, isocitrate dehydrogenase,  $\alpha$ -glycerophosphate dehydrogenase, glutamate oxalotransaminase. The results of her studies indicate substantial heterozygosity in the Cuchara Canyon and Sierra Madre Mts. populations. This supports the cline theory. These data are presented in the Appendix. Other populations have not been studied by electrophoresis. On the Western Slope, however, field observations of pairs *in copulo* indicate the absence of mixed phenotype pairs (*fide* Scott L. Ellis). This observation supports the sibling species theory, and that there is some sort of isolating mechanism between *nikias* and *electa*.

Along the Front Range, there are some localities where *hesperis* and *electa* fly together, but intermediates are not recorded, again supporting the sibling species theory.

Based upon the available data, one may draw the following conclusions: Within the central massif in Colorado, there is an unknown isolating mechanism that causes *electa* and *hesperis*, and *electa* and *nikias* to behave as sibling species. At the north' and south poles of the region under discussion, this isolating mechanism has broken down and we find heterozygous and polymorphic populations.



Fig. 14. *S. atlantis* dark disc female, V. Cuchara Canyon, Huerfano Co., Co., 3-4 viii 81.

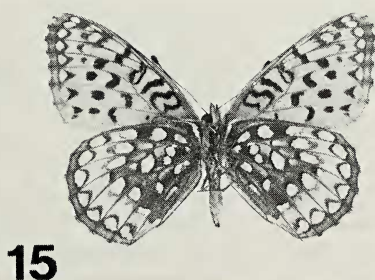


Fig. 15. *S. atlantis* dark disc female, V. Upper Sugarite Canyon, Las Animas Co., CO., 4-5 viii 81.

The *electa* phenotype apparently represents the parent *atlantis* stock. It prefers a boreal habitat, as is the case with nominate *atlantis*, other northern subspecies, and the Black Hills segregate. During the last ice age when boreal forest occupied what is now the Great Plains, there was

probably a single dark *atlantis* phenotype. Following the retreat of the glaciers and the resultant warming and drying out of the Plains, this entity found refugia in the Rocky Mts., the Black Hills, and the Canadian border states.

The pale phenotype *ratonensis* found in the Raton and Johnson Mesa area perhaps represents an offshoot of a pale species that occupied a more savanna-like environment in the Southwest during the last ice age. There are parallel forms in southern Utah and Nevada.

The origin of the *hesperis* phenotype is unclear. There are various races of opaque-spotted *atlantis* throughout the western United States. In the Black Hills, one such form (*lurana* dos Passos & Grey) is sympatric and synchronic with the dark-disc silvered form. Intermediates do occur, but they are not at all common. Both the silvered and unsilvered forms occur in about equal numbers at some localities. One can interpret the field data from the Black Hills as supporting the sibling species theory, rather than polymorphism in a single species produced, perhaps, by environmental factors.

Only carefully controlled rearing experiments in the laboratory, as noted previously, will resolve the questions that surround the *Speyeria atlantis* complex.

It should be noted that the division made by Howe (1975) of the *atlantis* complex into *atlantis* and *electa* is not correct based upon current knowledge. The *electa* phenotype belongs with nominate *atlantis*, while *hesperis* perhaps represents a sibling species.

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## Appendix

The data presented in Table 1 are excerpted from the work of Tebaldi (1982), p. 21). The *Speyeria atlantis* populations for which data are presented occur geographically as follows: (Battle Creek) Vic. Battle Creek Campground, Sierra Madre Range, ca. 7400' (2257 m), Albany Co., Wyoming. (Cuchara Canyon) Vic. Cuchara Canyon Campground, Spanish Peaks, ca. 9300' (2836 m), Huerfano Co., Colorado. The abbreviations used in the table are as follows: MDL = Malic dehydrogenase. ME = Malic enzyme. GDH = Glutamate dehydrogenase. IDH = Isocitrate dehydrogenase.  $\alpha$ GPdH =  $\alpha$ -glycerophosphate dehydrogenase. GOT = Glutamate oxalotransaminase. The subscripts designate different fractions of the related enzyme. *n* = the number of genomes sampled. *het* = the frequency of heterozygotes. *ca* = common allele. *N* = null allele. *sc* = slow common allele. *fc* = fast common allele. *s* = slow allele relative to the common allele *ca*. *f* = fast allele relative to the common allele *ca*. The terms "fast" and "slow" relate to the nature of the band separations in the electrophoresis method used for analysis.  $\bar{H}_L$  = average heterozygosity per locus.

Detailed interpretation and analysis of the enzyme electrophoresis separations summarized in Table 1 will be found in Tebaldi (1982). The data presented in Table 1 are for the combined phenotypes collected at each of the two geographic locations. The numbers of phenotypes collected at each location are as follows: Battle Creek. *nikias* 21, *electa* 22, *hesperis* 1, *nikias-electa* intergrade 3. Total = 47. Cuchara Canyon. *nikias* 51, *electa* 3, *hesperis* 9, *nikias-electa* intergrade 2, *nikias-hesperis* intergrade 3. Total = 68.



Table 1. Allele Frequencies and Observed Heterozygosity per Locus for Eleven Enzyme Loci in *Speyeria atlantis* (Combined Phenotypes) from Two Localities.\*

		Battle Creek	Cuchara Canyon			Battle Creek	Cuchara Canyon
<i>MDH</i> <sub>1</sub>	<i>n</i>	47	68	<i>IDH</i> <sub>2</sub>	<i>n</i>	47	64
	<i>het</i>	0.00	0.01		<i>het</i>	0.00	0.58
	<i>ca</i>	1.00	0.99		<i>sc</i>	1.00	0.55
	<i>f</i>	—	0.01		<i>fc</i>	—	0.40
<i>MDH</i> <sub>2</sub>	<i>n</i>	47	68	<i>IDH</i> <sub>2</sub>	<i>f</i>	—	0.04
	<i>het</i>	0.00	0.00		<i>s</i>	—	0.01
	<i>ca</i>	0.98	1.00		<i>n</i>	47	68
	<i>f</i>	0.02	—		<i>het</i>	0.02	0.18
<i>ME</i> <sub>1</sub>	<i>n</i>	46	52	<i>αGPdH</i>	<i>ca</i>	0.99	0.91
	<i>het</i>	0.00	0.58		<i>N</i>	0.01	0.03
	<i>sc</i>	1.00	0.56		<i>s</i> <sub>1</sub>	—	0.04
	<i>fc</i>	—	0.41		<i>s</i> <sub>2</sub>	—	0.02
	<i>f</i> <sub>1</sub>	—	0.01	<i>GOT</i> <sub>1</sub>	<i>n</i>	46	67
	<i>f</i> <sub>2</sub>	—	0.02		<i>het</i>	0.02	0.00
<i>ME</i> <sub>2</sub>	<i>n</i>	47	66		<i>ca</i>	0.99	1.00
	<i>het</i>	0.13	0.14		<i>s</i>	0.01	—
	<i>sc</i>	0.07	0.20		<i>n</i>	47	68
	<i>fc</i>	0.84	0.66		<i>het</i>	0.09	0.2
	<i>f</i>	—	0.06		<i>ca</i>	0.96	0.88
	<i>s</i>	0.09	0.08		<i>f</i>	0.02	0.07
<i>ME</i> <sub>3</sub>	<i>n</i>	46	67	<i>GOT</i> <sub>2</sub>	<i>s</i>	0.02	0.05
	<i>het</i>	0.00	0.12		<i>n</i>	45	67
	<i>ca</i>	1.00	0.92		<i>het</i>	0.00	0.00
	<i>s</i> <sub>1</sub>	—	0.01		<i>ca</i>	0.98	1.00
	<i>s</i> <sub>2</sub>	—	0.07		<i>s</i>	0.02	—
<i>GDH</i>	<i>n</i>	46	68	$\bar{H}_L$		0.027	0.166
	<i>het</i>	0.04	0.01				
	<i>ca</i>	0.98	0.99				
	<i>f</i>	0.01	0.01				
	<i>s</i>	0.01	—				

\*From Tebaldi (1982).